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THE CAROTID CIRCULATION IN THE RODENTIA

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No. 10 — *The Carotid Circulation in the Rodentia*

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CONTENTS

Introduction	457
Methods and Materials	458
Family Sciuridae	459
Family Gliridae	462
Family Ctenodactylidae	462
Family Muridae	462
Family Cricetidae	465
Family Zapodidae	468
Family Heteromyidae	469
Family Dipodidae	469
Family Castoridae	469
Suborder Caviomorpha	471
Family Hystriidae	472
Family Geomyidae	472
Family Bathyergidae	473
Family Pedetidae	474
Other Families	475
Fossil Forms	475
Embryology	476
Discussion	477
Summary	480
Literature Cited	481

INTRODUCTION

Tandler's studies of carotid arteries (1899, 1901) indicated that a great deal of variation exists in the cranial trunk arteries of rodents. The present study began as an attempt to discover the extent of this variation. It was hoped that this study might give some indication as to the interrelationships of the various groups of rodents whose phylogeny has not been determined from the fossil record.

The order in which the rodents are discussed in this paper is determined by similarities in arterial pattern, particularly with respect to the internal carotid artery, rather than by the order in which they are commonly placed in current classifications (e.g. Wood 1955). This grouping is one of descriptive convenience and does not necessarily indicate close relationship between groups adjacent in the text.

METHODS AND MATERIALS

The resources of the Mammalogy Department of the Museum of Comparative Zoology were made available to me, and skulls of all rodent genera in this collection were examined. In addition, preserved and fresh specimens of many species were injected with colored latex and dissected. Although a detailed description of the arterial and venous pathways was at first envisioned, this proved to be impractical as work progressed. Dissection of both sides of four latex-injected specimens of *Rattus*, four of *Sciurus*, and four of *Cavia* indicated that while the larger trunk arteries remain constant in their position in each species, the smaller arteries vary considerably in their position, pathways, and branching. Further, the venous system shows on an intraspecific level almost as much variation, even in the larger vessels, as is found between families. The arteries described here are the larger trunk arteries in which intraspecific variation is at a minimum.

The terminology used for familial and higher categories is that of Wood (1955); generic to subfamily names are from Simpson (1945); and specific names are from Ellerman (1940-41). The terminology of Greene (1935) is used for muscles and blood vessels except where noted in the text. The nomenclature used for foramina is essentially that of Hill (1935).

I wish to thank Miss Barbara Lawrence and Dr. Charles Lyman of the Museum of Comparative Zoology for allowing me the use of the collections of the Mammalogy Department, and Dr. Richard Van Gelder of the American Museum of Natural History, Professor Albert E. Wood of Amherst College, and Mr. Richard Thorington, Mr. Charles Mack, and Mr. Neal Todd of Harvard University for their generous donation of specimens for dissection. I am especially grateful to Professors Bryan Patterson and Albert E. Wood for their most helpful criticism of the manuscript of this paper.

SCIURIDAE

Tandler (1899) described the circulation in *Marmota* (*Arctomys* in his terminology) and in three species of *Sciurus*. The following description of carotid circulation is based on the dissection of four latex-injected specimens of *Sciurus carolinensis* (Fig. 1).

The common carotid artery divides into the external carotid and stapelial arteries at the level of the occipital condyle. The internal carotid artery is not found in adult *Sciurus*.¹

The external carotid artery passes forward dorsal to the hypoglossal nerve, digastric muscle, and hyoid apparatus, and gives rise to the occipital and superior thyroid arteries.² At the level of the tympanic bulla the external carotid gives rise to the common trunk of the lingual and external maxillary arteries, and then turns laterally and dorsally across the bulla towards the external auditory meatus. The external carotid gives rise to masseteric arteries and to the anterior and posterior auricular arteries during its course upward across the bulla. The external carotid divides into the superficial temporal and internal maxillary arteries near the auditory meatus.

The internal maxillary artery can be divided into three parts, the mandibular, pterygoid, and orbital portions (corresponding to the first, second, and third, or maxillary, pterygoid, and sphenomaxillary portions in man). The inferior alveolar and middle meningeal arteries branch from the first or mandibular portion of the internal maxillary artery, arising from this artery soon after its origin from the external carotid. The second or pterygoid portion of the internal maxillary artery gives rise to the arteries which accompany the anterior part of the mandibular division of the trigeminal nerve. The latter include the pterygoid, anterior and posterior deep temporal, and buccinator arteries, as well as a number of arteries to the masseter muscles. The third or orbital portion of the internal maxillary artery continues forward passing medially through an opening in the lateral pterygoid ridge and uniting with the medial or inferior portion of the stapelial artery. The orbital portion then continues forward through the alisphenoid canal entering the orbit through the

¹ Tandler states that the internal carotid exists only as the stem of the stapelial artery.

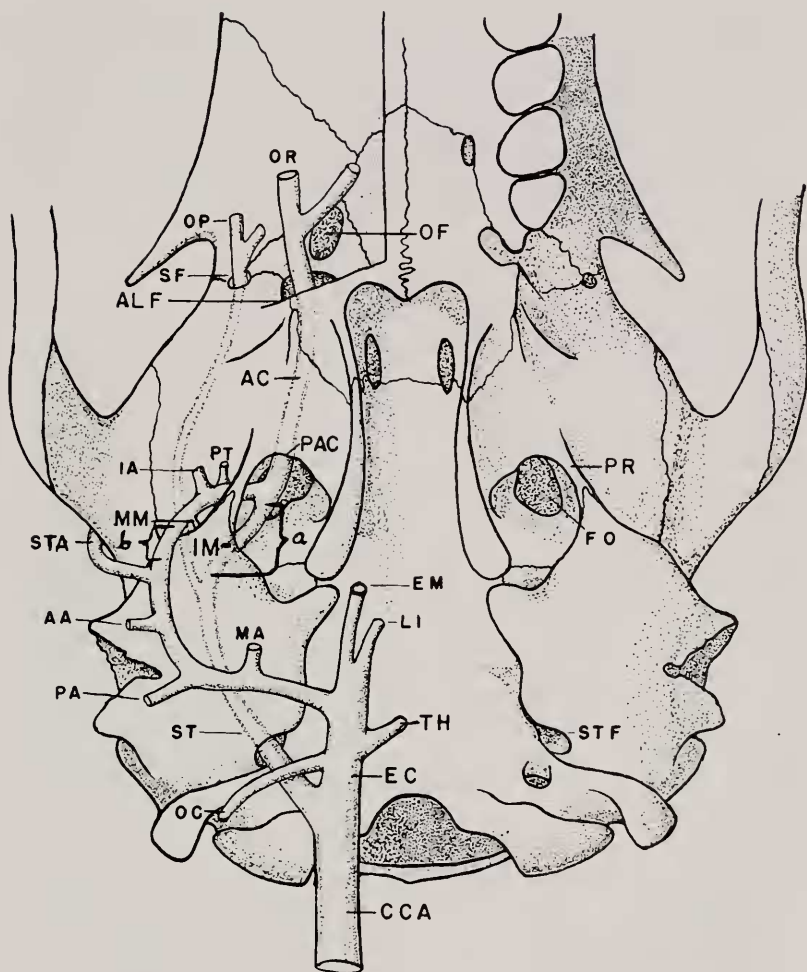
² The branches of the trunk arteries mentioned here are not the only branches that occur but rather the more important ones. They serve as markers for identifying and discussing the trunk arteries.

anterior lacerate foramen (sphenoidal fissure of Hill). In the orbit, the orbital portion gives rise to the infraorbital, sphenopalatine, descending palatine, and alveolar arteries.

The stapedia artery enters the tympanic bulla through the stapedia foramen and traverses the bulla enclosed in the stapedia canal which is ossified except in the vicinity of the stapes. While in the bulla this artery divides into two parts which Tandler named the superior and inferior portions. The more medial branch or inferior portion passes out of the bulla between the tympanic bulla and periotic capsule (petro-tympanic fissure), and onto the ventral surface of the skull where it unites with the internal maxillary artery. The more lateral branch or superior portion of the stapedia artery is the ophthalmic artery. It passes out of the bulla through the petro-tympanic fissure, but remains within the skull, passing forward between the squamosal and the dura mater. It enters the orbit through the sphenofrontal foramen, an opening in the suture between the frontal, squamosal, and alisphenoid bones. Tandler noted that in *Sciurus aureogaster* and in *Marmota* there is a rudimentary connection between the posterior communicating artery in the circle of Willis and the ophthalmic artery through the optic foramen.

In *Sciurus*, the main blood supply to the brain is carried by the two vertebral arteries. These arteries unite at the level of the foramen magnum to form the basilar artery. This artery enters

FIG. 1. *Sciurus carolinensis* $\times 5$, AA, anterior auricular artery; AC, alisphenoid canal; ALF, anterior lacerate foramen; CC, carotid canal; CCA, common carotid artery; EC, external carotid artery; EM, external maxillary artery; FO, foramen ovale; IA, inferior alveolar artery; IC, internal carotid artery; IM, internal maxillary artery; LI, lingual artery; MA, masseteric artery; MLF, middle lacerate foramen; MM, middle meningeal artery; OC, occipital artery; OF, optic foramen; OP, ophthalmic artery; OR, branches of the orbital portion of the internal maxillary artery; PA, posterior auricular artery; PAC, posterior opening to the alisphenoid canal; PLF, posterior lacerate foramen; PR, lateral pterygoid ridge; PT, branches of the pterygoid portion of the internal maxillary artery; SF, sphenofrontal foramen; ST, stapedia artery; STA, superficial temporal artery; STF, stapedia foramen; TH, superior thyroid artery. Elimination of the segment of the stapedia artery labelled *a* would result in a carotid pattern similar to that found in *Eliomys*. Elimination of the segment of the internal maxillary artery labelled *b* and the addition of an internal carotid artery would result in a carotid pattern similar to that found in *Mesocricetus*.



the skull through the foramen magnum passing ventral to the brain. Once in the skull the basilar artery divides into two large posterior communicating arteries. These pass forward on each side of the ventral surface of the brain and give rise to numerous small branches which pass into the brain. Just posterior and ventral to the olfactory lobes, the two posterior communicating arteries reunite. The ring formed by these arteries is the circle of Willis.

Skulls representing nearly every genus included in the family Sciuridae were examined. They all possess stapediai canals and sphenofrontal foramina and lack openings for the internal carotid artery. Although the presence of the connections between the internal maxillary artery and the stapediai artery and between the posterior communicating artery and the ophthalmic artery cannot be ascertained from skeletal material, the pattern described for *Sciurus* seems to be present throughout this family.

GLIRIDAE

Dissection of a latex-injected specimen of *Eliomys quercinus* indicates that this species has a carotid circulation very similar to that found in *Sciurus*. The only difference is the absence of the more medial or inferior portion of the stapediai artery in *Eliomys*. The stapediai artery exists only as the stem for the ophthalmic artery. There is no connection between the stapediai artery and the internal maxillary artery.

An examination of skeletal material indicates that the pattern found in *Eliomys* is present in *Dryomys* and in the subfamily Graphiurinae (*Graphiurus*), the skulls of these forms possessing stapediai canals and sphenofrontal foramina. However, in *Glis*, *Muscardinus*, and *Glirulus* these structures are not present. In these genera the ophthalmic artery must either arise from the orbital portion of the internal maxillary artery or from the posterior communicating artery in the circle of Willis. These are the only alternatives to a stapediai origin for the ophthalmic artery known to occur in the Mammalia.

CTENODACTYLIDAE

Dissection of a latex-injected specimen of *Pectinator sphenei* shows that the carotid circulation in this form is like that of *Eliomys* except that there is no trace of a stapediai artery. The ophthalmic artery arises from the orbital portion of the internal maxillary artery after the latter artery enters the orbit. The pattern in *Pectinator* is, therefore, possibly the same as that in *Glis*.

MURIDAE

The cranial arteries of *Rattus* were described by Tandler (1899) and by Greene (1935). The following description is based on these works and on the dissection of four latex-injected specimens of *Rattus norvegicus* (Fig. 2).

The carotid circulation in *Rattus* differs from that found in *Sciurus* in respect to the origin of the orbital portion of the internal maxillary artery, the origin of the ophthalmic artery, and in the presence of an internal carotid artery.

The common carotid artery divides at the level of the thyroid gland into the internal and external carotid arteries. The external carotid artery is similar to that described for *Sciurus*. The

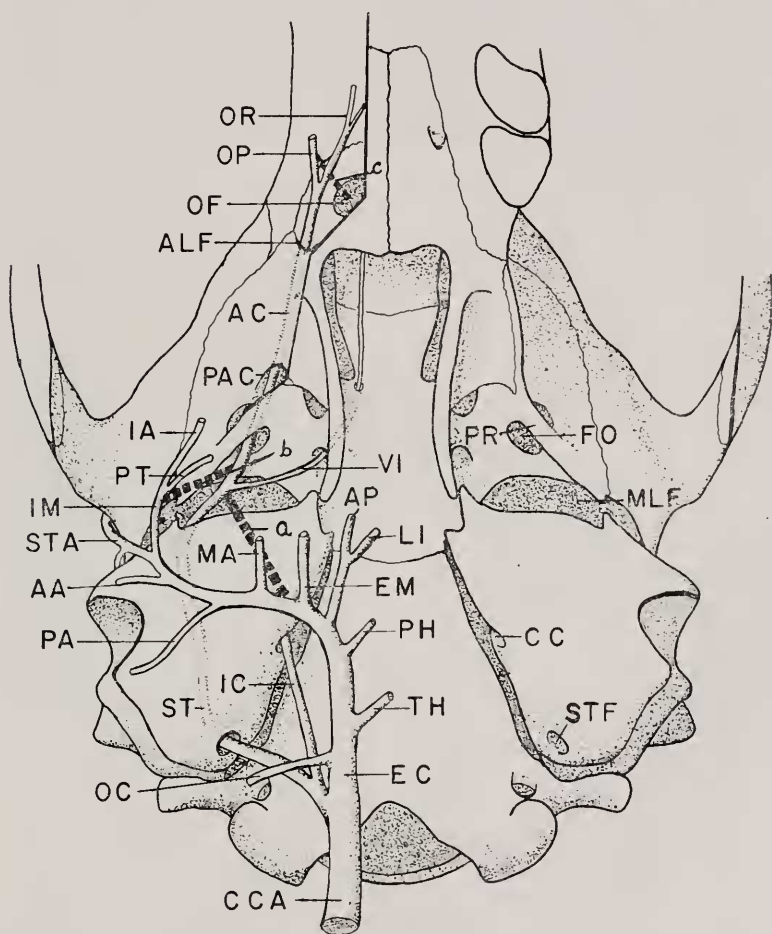


FIG. 2. *Rattus norvegicus* $\times 5$, AP, ascending palatine artery; PH, ascending pharyngeal artery; VI, vidian artery; for other abbreviations see Fig. 1. The dashed lines labelled a, b, and c, designate the courses of arteries found in the embryo of *Rattus* but not in the adult.

internal maxillary artery arises from the external carotid as it does in *Sciurus*. However, the internal maxillary artery gives rise only to branches of its pterygoid and mandibular portions. It has no connection with either the stapedia artery or with an orbital portion as it has in *Sciurus*.

The internal carotid artery gives rise to the stapedia artery (pterygopalatine artery of Greene) shortly after leaving the external carotid and then passes into the skull through a groove (carotid canal) on the medial side of the tympanic bulla joining the posterior communicating artery in the circle of Willis. The small size of this latter artery indicates that the internal carotid arteries, rather than the vertebral arteries, supply most of the blood to the brain.

Except for the connection with the internal carotid artery, the pattern of the circle of Willis is basically the same as that in *Sciurus*. However, because the internal carotid is so much larger than the posterior communicating artery, the former name is used for the artery in the circle of Willis anterior to where the internal carotid enters the circle of Willis.

The stapedia artery enters the tympanic bulla through the stapedia foramen. It traverses the bulla remaining completely enclosed in the stapedia canal which is ossified except in the vicinity of the stapes. This artery emerges on the anterior side of the bulla through the petro-tympanic fissure. Here it sends a small branch to the internal nares (palatine portion of the pterygopalatine artery or Vidian artery of Greene). The rest of the stapedia artery passes laterally through an opening in the lateral pterygoid ridge, passing over the foramen ovale, and enters the alisphenoid canal. It remains in this canal until it reaches the anterior lacerate foramen through which it enters the orbit. Once in the orbit the stapedia artery divides into several branches. These are the ophthalmic artery and the branches of the orbital portion of the internal maxillary artery.

It was determined by dissection that *Mus musculus*, *Aethomys kaiseri*, and *Dasymys incomitus medius* have the same arterial pattern as that described for *Rattus*. From the presence of canals for the stapedia and internal carotid arteries in other genera it appears that this pattern is present throughout the Muridae. Some variation occurs in this family in the amount of ossification of the alisphenoid and stapedia canals and in the position of the posterior opening of the alisphenoid canal, but these differences do not affect the carotid pattern.

CRICETIDAE

As a great deal of variation occurs within this family, the Cricetidae will be treated by subfamilies.

MICROTINAE and GERBILLINAE

The following description is based on the dissection of a latex-injected specimen of *Microtus pennsylvanicus* (Fig. 3).

The common carotid artery divides at the level of the occipital condyle into the external and internal carotid arteries. The external carotid artery is similar to that described for *Sciurus* except in its relation to the internal maxillary artery. The latter artery, as a branch of the external carotid, is very reduced,

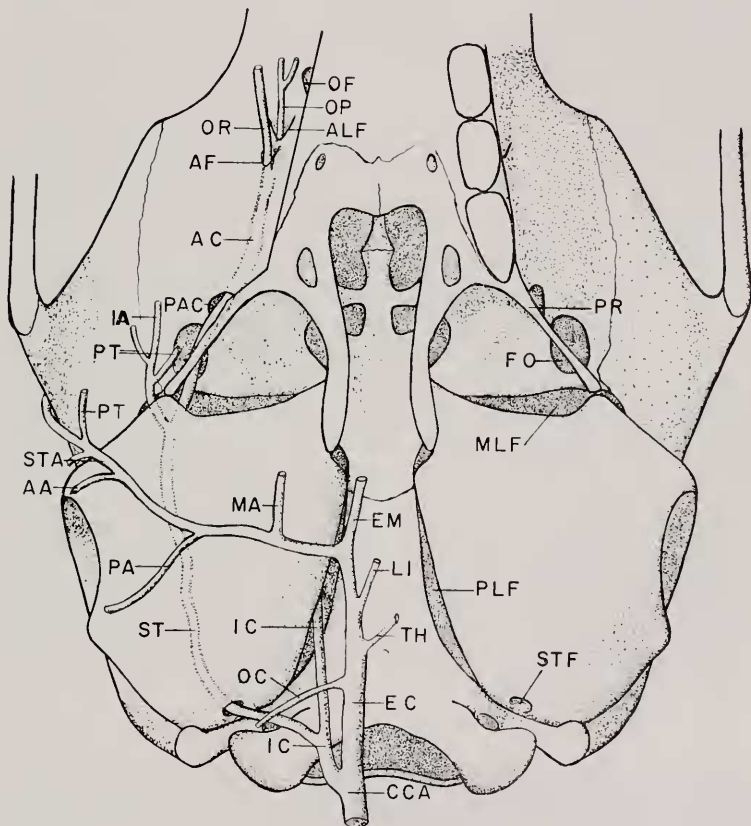


FIG. 3. *Microtus pennsylvanicus* $\times 6.5$, for abbreviations see Fig. 1.

consisting only of a few branches of its pterygoid portion. These arise separately from the external carotid and supply the masseter, buccinator, and temporal muscles.

The internal carotid artery gives rise to the stapedia artery soon after leaving the common carotid and continues into the skull through the posterior lacerate foramen (jugular foramen of Hill) joining the posterior communicating artery in the circle of Willis. The circle of Willis is similar to that found in *Rattus* except that the vertebral arteries are the same size as the internal carotid arteries.

The stapedia artery enters the bulla through the stapedia foramen. While in the bulla this artery sends branches (not shown in Fig. 3) dorsally through the petro-tympanic fissure to the dura mater. A few branches also reach the temporal muscle through openings in the suture between the squamosal and parietal bones. Near the anterior end of the bulla the stapedia artery gives rise to the inferior alveolar artery. This artery passes laterally through the petro-tympanic fissure and the middle lacerate foramen to the mandible. The inferior alveolar artery plus the smaller branches of the stapedia artery in the bulla correspond to the branches of the mandibular portion of the internal maxillary artery.

The stapedia artery passes through the petro-tympanic fissure medial to the lateral pterygoid ridge. Arteries corresponding to part of the pterygoid portion of the internal maxillary artery may arise either here or in common with the inferior alveolar artery as shown in Figure 3. The stapedia artery continues forward through an opening in the lateral pterygoid ridge and enters the skull again through a small foramen. This opening corresponds to the posterior end of the alisphenoid canal in *Sciurus* and *Rattus*. This canal is not ossified in *Microtus*. The stapedia artery emerges into the orbit through its own foramen, termed the alisphenoid foramen by Hill (1935),³ and branches extensively. The branches correspond to those of the orbital portion of the internal maxillary artery as described in *Sciurus*.

The ophthalmic artery is a branch of the stapedia artery,

³ The alisphenoid foramen is actually the lateral part of the anterior lacerate foramen. In *Clethrionomys* the posterior cheek teeth and the maxillary bones surrounding them extend up into this latter opening giving it the shape of an inverted U. In *Microtus* the cheek teeth extend farther upward and the maxillary bone surrounding them has fused with the frontal bone. This divides the anterior lacerate foramen into two parts, the more lateral of which is the alisphenoid foramen.

arising just before the latter artery enters the orbit. The ophthalmic artery enters the orbit through the anterior lacerate foramen or, in some cases, through a sphenofrontal foramen.

Dissection of a latex-injected specimen of *Clethrionomys gapperi* and examination of skulls of the other genera belonging to the subfamilies Microtinae and Gerbillinae indicates that the carotid circulation throughout these groups is basically the same as that described for *Microtus*. Although the sphenofrontal and alisphenoid foramina were not present and the foramen ovale and posterior opening of the alisphenoid canal were confluent in many genera, these differences do not affect arterial pattern.

CRICETINAE

Latex-injected specimens of *Peromyscus leucopus* and *Mesocricetus auratus* were dissected. The arterial pattern found in these genera is basically the same as that described for *Microtus*. Differences do occur, however, in the origin of the ophthalmic artery and in the course of the stapedia artery. An alisphenoid foramen is not found in this group; the stapedia artery enters the orbit through the anterior lacerate foramen, as in *Clethrionomys*. In both *Peromyscus* and *Mesocricetus* the ophthalmic artery branches from the stapedia artery within the tympanic bulla, passing forward into the orbit through the sphenofrontal foramen in the same manner as has been described for *Sciurus*.

Mesocricetus differs from both *Microtus* and *Peromyscus* in that the branches of the stapedia artery corresponding to the mandibular and pterygoid portions of the internal maxillary artery separate from the stapedia artery after it has emerged from the bulla rather than within the bulla.

When the ophthalmic artery originates from the stapedia artery within the bulla, as it does in *Sciurus*, *Eliomys*, *Peromyscus*, and *Mesocricetus*, there is usually a groove on the inner surface of the squamosal bone indicating its passage. Most members of the tribe Hesperomyini and all the members of the tribe Cricetini have this groove and stapedia canals. These rodents probably have a carotid circulation similar to that described for *Peromyscus*. However, in the tribe Myospalacini and in some members of the Hesperomyini, notably *Neotoma*, this groove is absent and the stapedia canal is occluded in the adult.⁴ In these forms which lack a stapedia artery in the adult the carotid

⁴ The sphenofrontal foramen was not found in any specimen of *Neotoma* examined, although Hill (1935) states that it is present in this genus.

pattern is presumably similar to that described for *Glis* and *Pectinator* with the addition of an internal carotid artery.

In the Platacanthomyini, as in the Hesperomyini, the carotid pattern is variable. *Typhlomys* has a stapedia canal, sphenofrontal foramen, and a groove between these structures indicating a stapedia origin for the ophthalmic artery. *Platacanthomys* lacks these structures. This indicates that *Typhlomys* has a carotid pattern similar to that of *Peromyscus* while the pattern found in *Platacanthomys* is similar to that of *Neotoma* or *Glis*.

NESOMYINAE

The skulls of the members of this group show variation similar to that found in the Platacanthomyini and the Hesperomyini. *Nesomys* has a stapedia canal, sphenofrontal foramen and alisphenoid canal, and probably has a carotid circulation similar to that found in either *Mesocricetus* or *Peromyscus*. *Eliurus*, *Brachyuromys* and *Brachytarsomys* lack the sphenofrontal foramen and while traces of the stapedia canal are present, the canal is occluded. The latter forms probably have a carotid pattern similar to that described for *Glis* with the addition of an internal carotid artery.

LOPHIOMYINAE

Lophiomyia also lacks a functional stapedia canal in the adult and probably has a carotid circulation similar to that found in *Glis* with the addition of an internal carotid artery.

ZAPODIDAE

A latex-injected specimen of *Napcozapus insignis* was dissected and skulls of *Zapus* and *Sicista* were examined. The arterial pattern in this group is basically the same as that found in *Microtus*. Both internal carotid and stapedia arteries are present in *Napcozapus*, the latter giving rise to the ophthalmic artery and to all of the internal maxillary circulation.

Minor differences occur in the course of the stapedia artery because of the shape of the basiscranial region. The stapedia artery does not pass onto the ventral surface of the skull after leaving the tympanic bulla, but remains within the skull until reaching the orbit which it enters through the anterior lacerate foramen. Branches corresponding to the mandibular and pterygoid portions of the internal maxillary artery arise from the

stapedial artery just anterior to the tympanic bulla and pass ventrally through the middle lacerate foramen. Branches corresponding to the orbital portion of the internal maxillary artery and to the ophthalmic artery arise from the stapedial artery once the latter artery has entered the orbit.⁵

HETEROMYIDAE

Dissection of a latex-injected specimen of *Dipodomys spectabilis* reveals a carotid pattern similar to that of *Napeozapus*. The only difference is the existence of a slender connection between the external carotid artery and the pterygoid portion of the internal maxillary artery, the latter arising from the stapedial artery in *Dipodomys* as it does in *Napeozapus*. This connection branches from the external carotid in the area from which the internal maxillary artery arises in *Rattus* and *Sciurus*.

The foramina in the skulls of *Perognathus* and *Microdipodops* are the same as those found in *Dipodomys*. *Liomys* and *Heteromys* lack a stapedial foramen and canal, although an alisphenoid canal is present in these forms. The circulation in these genera may be similar to that found in *Geomys* or to that found in *Glis* with the addition of an internal carotid artery.

DIPODIDAE

Examination of the skulls of *Dipus*, *Jaculus*, *Scirtopoda*, *Allactaga*, *Pygeretmus*, and *Euchoreutes* indicates that the foramina pattern is uniform throughout this family. An internal carotid canal and a well-ossified stapedial canal are present in these genera. Apparently the stapedial artery does not pass ventrally through the middle lacerate foramen but remains within the skull until reaching the orbit which it enters through the anterior lacerate foramen. The condition of the inferior alveolar artery and the ophthalmic artery cannot be determined from skeletal material. However, the configuration of the foramina and the shape of the skull suggests a carotid pattern similar to that of the Zapodidae.

CASTORIDAE

The carotid circulation described below is based on the dissection of a latex-injected specimen of *Castor canadensis* (Fig. 4).

⁵ The sphenofrontal foramen was not found in any members of the genus *Zapus* examined, although Hill (1935) states that it is present in *Z. princeps*.

The common carotid artery divides into internal and external carotid arteries at the level of the occipital condyle. The external carotid artery is similar in condition to that found in *Sciurus* and *Rattus* except in its relation to the internal maxillary artery.

Although the internal maxillary artery is a branch of the external carotid, it is not one of the terminal branches of this artery as it is in *Sciurus*. Rather, it leaves the external carotid soon after the latter gives rise to the external maxillary artery, and before the external carotid gives rise to the posterior auricular artery. The internal maxillary artery passes ventrally and anteriorly to the area anterior to the bulla passing just anterior to the internal pterygoid muscle. Once near the ventral surface of the skull it gives rise to a well developed mandibular portion which includes both inferior alveolar and middle meningeal arteries, the latter entering the skull through the middle lacerate foramen. The pterygoid portion of the internal maxillary, except for the buccinator and masseteric arteries, also arises here. The buccinator and masseteric arteries arise farther forward and pass laterally

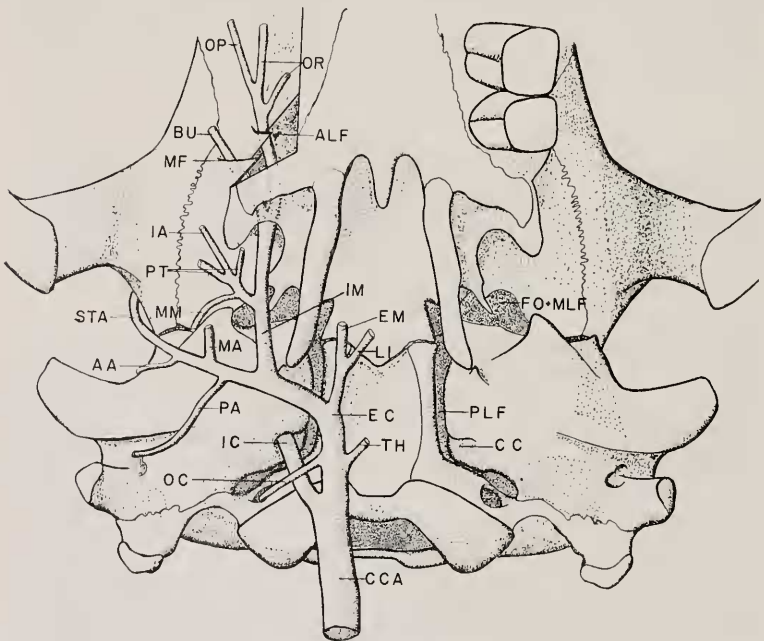


FIG. 4. *Castor canadensis* $\times 1.4$, BU, buccinator and masseteric arteries; MF, masticatory foramen; for other abbreviations see Fig. 1.

through the masticatory foramen in company with the anterior portion of the mandibular trunk of the trigeminal nerve.⁶ The orbital portion of the internal maxillary artery continues through the alisphenoid canal into the orbit. The ophthalmic artery arises from the orbital portion of the internal maxillary artery within the orbit.

The internal carotid enters the skull through a groove (carotid canal) on the medial side of the bulla and joins the posterior communicating artery in the circle of Willis. The size of the internal carotid arteries indicates that they, rather than the vertebral arteries, supply most of the blood to the brain. The circle of Willis in *Castor* is similar to that described for *Rattus*.

CAVIOMORPHA

Tandler described the carotid circulation of *Cavia porcella* (1899) and *Lagostomus maximus* (1901). Reference to these descriptions, dissection of latex-injected specimens of *Cavia*, *Myoprocta*, and *Plagiodontia*, and examination of skulls of nearly all the living genera in this group indicates that the same carotid pattern is present throughout the Caviomorpha. For this reason this suborder is treated as one unit.

The common carotid artery continues forward as the external carotid artery. The stapedia artery is not present in adults although a trace of the stapedia canal is often found, indicating the presence of this artery in the embryo. Similarly, although the internal carotid artery is absent in adult members of this suborder, Tandler (1899) noted its presence in the embryo of *Cavia*.

The external carotid artery in the Caviomorpha resembles that described for *Castor*, although in some cases the lingual, external maxillary, and internal maxillary arteries were observed to arise in common from the external carotid artery. The mandibular and pterygoid portions of the internal maxillary artery differ in the Caviomorpha somewhat from the condition found in *Castor* in that they arise separately from the internal maxillary artery instead of from a common trunk as in *Castor*.

In the forms dissected, the ophthalmic artery is formed by the union of a branch from the orbital portion of the internal maxillary artery and a branch from the posterior communicating artery, the latter entering the orbit through the optic foramen.

⁶ The masticatory foramen is often confluent with the anterior lacerate foramen.

The circle of Willis in the Caviomorpha is similar to that described for *Sciurus*.

HYSTRICIDAE

The carotid pattern in this family appears, from Tandler's (1901) description of *Hystrix cristata*, to be the same as that found in the Caviomorpha. The only difference is the presence in adult *Hystrix* of a rudimentary internal carotid artery. This artery is apparently vestigial in nature, reaching the carotid canal but not remaining open as far as the posterior communicating artery in the circle of Willis. A strand of tissue marks its connection with the latter structure.

GEOMYIDAE

A latex-injected specimen of *Geomys bursarius* was dissected and skulls of the other members of this family were examined. The following description is of the carotid pattern found in *Geomys*.

The common carotid artery continues anteriorly as the external carotid artery. The internal carotid and stapedia arteries are not present. The external carotid artery in *Geomys* is similar to that described for *Sciurus* except in its relation to the internal maxillary artery.

The pterygoid and mandibular portions of the internal maxillary artery, the mandibular portion consisting chiefly of the inferior alveolar artery, arise from the end of the external carotid artery as they do in *Rattus* and *Sciurus*. The orbital portion of the internal maxillary artery arises in common with the common trunk of the lingual and external maxillary arteries. This is the position from which the whole internal maxillary originates in the Caviomorpha and in *Castor* and *Hystrix*. The orbital portion courses forward turning dorsally towards the basiscranial region in front of the internal pterygoid muscle. Just before the orbital portion enters the alisphenoid canal it receives a small branch from the pterygoid portion of the internal maxillary artery. The orbital portion enters the orbit through the anterior lacerate foramen and gives rise to the ophthalmic artery within the orbit. The circle of Willis in *Geomys* is similar to that described for *Sciurus*.

Many skulls of *Geomys* and of the other genera in this family have a small indentation on the tympanic bulla in the position of a stapedia foramen, and in most of the geomyids the stapedia

The external carotid continues forward along the course taken by the internal maxillary artery in *Castor* and the Caviomorpha, passing dorsally anterior to the internal pterygoid muscle. Just anterior to the bulla the external carotid gives rise to the internal maxillary artery. The external carotid continues laterally and dorsally to the mandible reaching the dorsal surface of the skull behind the glenoid fossa. During its upward course the external carotid anastomoses with a slender branch from the posterior auricular artery and gives rise to masseteric, anterior auricular, temporal, and superficial temporal arteries.

The internal maxillary artery divides into two portions soon after separating from the external carotid. The more lateral of these gives rise to the branches of the pterygoid and mandibular portions, the latter consisting of the inferior alveolar artery and a middle meningeal artery which enters the skull through the middle lacerate foramen. The more medial branch is the orbital portion of the internal maxillary. It enters the short alisphenoid canal emerging into the orbit through the anterior lacerate foramen.

The ophthalmic artery has a dual origin from the orbital portion of the internal maxillary artery and from the posterior auricular artery in the circle of Willis connecting with the latter through the optic foramen. The circle of Willis in this genus is similar to that described for *Sciurus*.

Cryptomys differs from *Bathyergus* only in that it lacks the connection between the posterior auricular artery and the anterior part of the external carotid artery.

PEDETIDAE

The carotid arteries of *Pedetes caffer* were described by Tandler (1899). The description here presented is based on Tandler's work and on the dissection of an uninjected late fetus of this species.

The common carotid artery divides at the level of the larynx into the external and internal carotid arteries. The external carotid artery is similar to that described for *Sciurus* except that it does not give rise to any part of the internal maxillary artery.

The internal carotid artery passes through the carotid canal into the skull to join the posterior communicating artery in the circle of Willis. There is no stapedia artery in *Pedetes*.

The internal maxillary artery arises from the internal carotid artery after this artery has entered the circle of Willis. It

divides within the skull into two portions, the posterior part leaving the cranial cavity in company with the mandibular portion of the trigeminal nerve through the foramen ovale. This portion corresponds to the mandibular and pterygoid divisions of the internal maxillary. The more anterior portion enters the orbit through the anterior lacerate foramen and corresponds to the orbital portion of the internal maxillary artery.

The ophthalmic artery arises separately from the internal carotid artery in the circle of Willis and enters the orbit through the optic foramen. The circle of Willis itself is similar in form to that found in *Rattus*.

OTHER FAMILIES

It was not possible to obtain preserved members of the families Rhizomyidae, Spalacidae, Anomaluridae, Petromuridae, Thryonomyidae, and Aplodontidae. However, some indication of the carotid circulation in these forms was obtained from skeletal material. The skulls of *Aplodontia*, *Petromus*, and *Thryonomys* lack stapelial canals and openings for the internal carotid arteries. Although the carotid pattern in these genera could be similar to that described for *Glis* or *Bathyergus*, the relationships suggested in current classifications (e.g. Wood 1955, Simpson 1945) for these genera would favor their possessing a carotid pattern similar to that found in *Castor*, *Hystrix*, and the Caviomorpha.

The skulls of members of the families Anomaluridae, Spalacidae, and Rhizomyidae possess openings for an internal carotid artery but lack stapelial canals. The basic carotid circulatory pattern in these forms could be like that of *Glis*, *Castor*, or *Pedetes*. On the basis of current classifications it is suspected that the Anomaluridae possess a carotid circulation similar to that of *Pedetes*, and that the Rhizomyidae and Spalacidae possess a pattern similar to that of either *Neotoma* or *Glis*.

FOSSIL FORMS

None of the fossil rodent skulls examined or figured in the literature possesses well preserved or carefully cleaned basi-cranial regions. Wood (1962) identifies a sphenofrontal foramen in *Paramys delicatus* indicating the presence of a stapelial artery in this form. *Reithroparamys* lacks a stapelial foramen and appears not to have had a stapelial artery. All the paramyids possess alisphenoid and internal carotid canals.

Sciuravus (Dawson 1961) lacks a stapedia foramen but appears to have a large opening for the internal carotid artery. *Ischyromys* also lacks a stapedia canal.

EMBRYOLOGY

Tandler (1902) described the development of the carotid circulation in *Rattus*. This is the only rodent on which such a study has been made. In the embryo of *Rattus* Tandler found a number of arteries not present in the adult. One of these arteries (*a* in Fig. 2) follows the course taken by the internal maxillary artery in *Castor* connecting the stapedia artery with the external carotid artery. Another embryonic artery follows the course taken by the internal maxillary artery found in *Pedetes* connecting the stapedia artery with the internal carotid artery through the foramen ovale. A third embryonic connection (*b* in Fig. 2) is found between the stapedia artery and the pterygoid portion of the internal maxillary (a branch of the external carotid in *Rattus*). Finally, there is a connection between the ophthalmic artery and the internal carotid artery in the circle of Willis in embryos of *Rattus* (*c* in Fig. 2). Almost all the carotid circulatory patterns found in the Rodentia can be formed from the arterial pattern present in the embryo of *Rattus* by using certain arteries and eliminating others.⁷

Whether or not all the arteries present in the embryo of *Rattus* are present in the embryos of other rodents is not known. However, as noted in the text, traces of a stapedia canal and internal carotid arteries are found in genera not possessing these arteries in the adult.

There are only a few cases where dual origins for arteries are retained in the adult animals, and in these instances one artery is usually smaller than the other. Thus, in the forms which retain dual origins for the ophthalmic artery, one of the two arteries usually carries most of the blood, while the other is reduced in size. Similarly, the connections between the pterygoid portion of the internal maxillary and the stapedia artery in *Sciurus* and the posterior communicating artery in *Rattus* are small vessels carrying little blood.⁸

⁷ The only artery not found in the embryo of *Rattus* is one corresponding to the stapedia origin of the ophthalmic artery as found in *Sciurus*, *Eliomys*, etc.

⁸ Injection of latex under pressure swells the arteries abnormally and may make these connections appear larger than they really are.

DISCUSSION

The possibility of variation in carotid circulatory pattern and of the parallel development of similar patterns in isolated groups of rodents is great and makes the value of differences in carotid patterns in determining relationship very indefinite. A knowledge of the genetic control of variation of carotid pattern and of the embryological development of the different patterns would be necessary in order to use differences in pattern confidently as an indicator of phylogenetic relationship. Nevertheless, the variation observed in carotid patterns leads to speculation as to the relationship between the various groups of rodents.⁹

The path followed by the external carotid artery is the same in all rodents examined with the exception of the Bathyergidae. The failure of the external carotid artery to pass laterally over the tympanic bulla in this family may be due to a difference in the shape of the skull. However, the fact that the posterior auricular artery and the thin connection between this artery and the external carotid artery (Fig. 5) take the course normally followed by the external carotid artery suggests that the difference in the course of the external carotid artery in the Bathyergidae is not due just to a simple shift in the position of the artery. The path that the external carotid artery takes in the Bathyergidae is initially the same as that which the internal maxillary artery follows in *Castor*. This suggests that the external carotid in adult Bathyergidae may be derived from other embryonic arteries. A study of the embryonic development of the cranial arteries in the Bathyergidae will be necessary to determine this.

The origins and pathways of four of the other arteries mentioned in this paper vary considerably within the Rodentia. The internal carotid artery varies in its presence in the Rodentia. When present this artery carries the main supply of blood to the brain. When the internal carotid is absent, the vertebral arteries supply the brain with blood. The stapedia artery varies in its presence and in which vessels it supplies. When present the stapedia artery supplies blood to all or part of the internal maxillary artery or to the ophthalmic artery or to both of these arteries. The ophthalmic artery varies in its origin in the

⁹ It should be noted that the variation in carotid pattern is most readily explainable in terms of Wood's classification of the Rodentia (1955). The groupings used in Schaub's (1958), Simpson's (1945), and earlier classifications of the rodents do not coincide with groupings made on the basis of carotid circulation. For this reason Wood's classification is used throughout this discussion.

Rodentia. It may originate from the internal carotid artery or posterior communicating artery in the circle of Willis as in *Pedetes* or *Hystrix*, or from the orbital portion of the internal maxillary artery or from vessels corresponding to this artery as in *Rattus* or *Pectinator*.¹⁰ The ophthalmic artery may also arise from the stapedia artery within the tympanic bulla as it does in *Sciurus*. If the latter origin occurs, the ophthalmic artery usually enters the orbit through a sphenofrontal foramen. In many cases the ophthalmic artery has a dual origin.

The internal maxillary artery varies in its origin and consequently in its pathway. This artery may arise wholly or in part from four different positions. The internal maxillary artery may arise from the stapedia artery as in *Microtus*, from the internal carotid artery as in *Pedetes*, from the anterior end of the external carotid artery as in *Pectinator*, or from a more posterior position on the external carotid artery as in *Castor*. The internal maxillary artery often arises from a combination of two of these positions. The variation of these arteries is summarized in Table 1.

TABLE 1

	internal carotid artery	origin of the ophthalmic artery	origin of the internal maxillary artery
Sciuridae	—	ST ± CW	ST + ECA
Ctenodaectylidae	—	OR	ECA
Bathyergidae	—	OR + CW	ECP
Hystriidae	—	OR + CW	ECP
Thryonomyidae	—	OR + CW?	ECP?
Petromuridae	—	OR + CW?	ECP?
Caviomorpha	—	OR + CW	ECP
Castoridae	+	OR	ECP
Apodontidae	—?	OR + CW?	ECP?
Geomyidae	—	OR	ECP + ECA
Heteromyidae	+	OR	ST or ECA
Dipodidae	+	OR	ST
Zapodidae	+	OR	ST
Spalacidae	+	OR?	ECA?
Rhizomyidae	+	OR?	ECA?
Muridae	+	OR	ECA and ST
Cricetidae	+	OR or ST	ECA and/or ST
Gliridae	—	OR or ST	ECA
Pedetidae	+	CW	CW
Atomaluridae	+	CW?	CW?

Abbreviations: CW, circle of Willis (see footnote 10); ECA, external carotid artery, anterior end; ECP, external carotid artery, posterior position; OR, orbital portion of the internal maxillary artery (see footnote 10); ST, stapedia artery.

¹⁰ The origin of the ophthalmic artery in *Hystrix* is the same as in *Pedetes*. The name of the trunk artery differs as discussed in relation to *Rattus*. Similarly, the origin of the ophthalmic artery is the orbital portion of the internal maxillary artery in both *Rattus* and *Pectinator*. However, the orbital portion is supplied by different trunk arteries in these two genera.

There seem to be three basic carotid patterns present in the Rodentia. The distinction between these patterns is most evident in the differences in origin of the internal maxillary artery. One pattern is that found in *Pedetes* where the internal maxillary artery originates from the internal carotid artery. This pattern is found in no other rodent group with the possible exception of the Anomaluridae. The great difference between this pattern and the patterns found in other rodents may indicate that the Pedetidae are a very ancient group. On the other hand, the great inflation of the bulla in *Pedetes* may prevent the development of the arterial patterns found in other rodents and necessitate the use of the internal carotid artery in carrying blood to the anterior part of the head. A study of the embryology of *Pedetes* will be necessary to determine which of these explanations is correct.

The second basic pattern is actually a combination of two patterns, that in which the internal maxillary artery or parts of it originate from the stapedia artery, and that in which the internal maxillary artery or parts of it originate from the anterior end of the external carotid artery. The presence of both these origins for the internal maxillary artery in *Sciurus*, the Heteromyidae, and in certain subfamilies of the Cricetidae necessitates the grouping together of these patterns. The pattern found in *Sciurus* can easily be changed either into a pattern similar to that found in *Eliomys* by the loss of a short section of the stapedia artery (*a* in Fig. 1), or into a pattern similar to that found in *Mesocricetus* by the loss of a short section of the internal maxillary artery (*b* in Fig. 1). The differences in carotid pattern within the Gliridae, Heteromyidae, and Cricetidae do not coincide with the divisions of these families made in current classifications. This may indicate that these families are in need of taxonomic revision but a more extensive study would be necessary to determine this.

The second basic pattern is found in every member of the suborder Myomorpha as well as in the families Sciuridae and Ctenodactylidae. The lack of a stapedia artery in *Sciuravus* eliminates this form from the direct ancestry of the Myomorpha but does not eliminate the possibility of a sciuravid origin for the Myomorpha as proposed by Wood (1959). The similarity of the pattern found in the Sciuridae to that found in the Myomorpha is an example of parallelism; this group originated from the Paramyidae and not the Sciuravidae (Wood 1959). The resemblance between the patterns found in the Sciuridae and Ctenodactylidae may indicate a common origin for these two groups as suggested by Wood (1955).

The third basic pattern is that in which the internal maxillary artery arises from the external carotid artery before the latter artery turns laterally across the tympanic bulla. This pattern or variations on it is probably found in all members of the suborders Caviomorpha, Hystricomorpha, Bathyergomorpha, Castorimorpha, and in the families Aplodontidae and Geomyidae. All the rodents in this group lack a stapedia artery and all except the Geomyidae and Castoridae have a dual origin for the ophthalmic artery as indicated in Table 1. According to Wood (1959) all these groups except the Geomyidae have arisen from the Paramyidae. The presence of this pattern in the Geomyidae is unexpected. However, this artery is present in the embryo of *Rattus* and probably in the embryos of most rodents. The dissection of one specimen of *Geomys* and one specimen of *Dipodomys* certainly is not enough to determine the closeness of the carotid pattern of the Geomyidae to that of the Heteromyidae, nor is it enough to determine which basic pattern is the primitive one in this group. Certainly this problem should be studied further.

The pattern found in the Castoridae differs from that found in other members of this group in both the absence of a connection between the ophthalmic artery and the circle of Willis and in the presence of an internal carotid artery. The Bathyergidae, as previously noted, differ from other rodents in the path taken by the external carotid artery. These differences as well as the geographic isolation of the Hystricomorpha from the Caviomorpha (Wood and Patterson 1959) indicate the probability of separate origins of the suborders included in this group from the Paramyidae.

A uniform ancestral pattern within the Rodentia may never have occurred in adult rodents but only in their embryos. The presence of the third pattern in many descendants of the paramyids as well as the evidence for the presence of a stapedia artery in this group may indicate that more than one basic pattern was present in adult members of the Paramyidae.

SUMMARY

The major variations of the carotid circulatory pattern in the Rodentia are described, these differences in pattern occurring mostly at or above the family level. Variations in pattern are attributed to the retention of different combinations of embryonic arteries in different groups of rodents. Reduction to one origin for each artery from the multiple origins found in the embryo

usually occurs, but whether one pattern has any advantage over another is not known. The variation in circulatory pattern found in the Rodentia may eventually be useful in determining phylogeny, but further work on the extent and embryological development of this variation must be done before the significance of variation in carotid pattern can be properly assessed.

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